EXPERIMENTAL ZOOGEOGRAPHY OF ISLANDS: DEFAUNATION AND MONITORING TECHNIQUES

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Abstract. In order to facilitate experiments on colonization, a technique was developed that permits the removal of the faunas of very small islands. The islands are covered by a tent and fumigated with methyl bromide at concentrations that are lethal to arthropods but not to the plants.

Seven islands in Florida Bay, of varying distance and direction from immigrant sources, were censused exhaustively. The small size (diameter 11–18 m) and ecological simplicity of these islands, which consist solely of red mangrove trees (*Rhizophora mangle*) with no supratidal ground, allowed the location and identification of all resident species. The terrestrial fauna of these islands is composed almost exclusively of arboreal arthropods, with 20–50 species usually present at any given moment. Surveys of these taxa throughout the Florida Keys, with emphasis on the inhabitants of mangrove forests, were made during 1967 in order to estimate the size and composition of the "species pool."

The seven experimental islands were defaunated in late 1966 and early 1967, and the colonists were monitored for 17–20 man-hours every 18 days. Precautions were taken to avoid artificial introductions during the monitoring periods.

INTRODUCTION

The first attempt to formulate a quantitative theory which would unite an ever-increasing mass of insular biogeographic data was made by MacArthur and Wilson (1963, 1967), who postulated an equilibrium number of species on an island determined by the intersection of immigration and extinction curves drawn as a function of the number of species already present. In addition to speculation on the forms of these curves and effects of varying both island area and distance from the source, they derived the equation

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$$t_{0.90} = 1.15 \frac{\text{mean } \check{S}}{X} \qquad (1)$$

where $\check{S}_i$ = the hypothetical equilibrium number of species on an island
mean $\check{S}$ = the mean of $\check{S}_i$ for a number of very similar islands i
X = the extinction rate (or turnover rate, since an equilibrium requires that extinction = immigration) in number of species per time at equilibrium
$t_{0.90}$ = time required for number of species present to increase from 0 to 90% of $\check{S}$.

Later the same authors elaborated upon the general shapes of immigration and extinction curves, discussed colonization rates and curves, and predicted the distribution of survival times of species that succeed in colonizing an island (MacArthur and Wilson 1967).

Data to test these hypotheses are scarce. Most biogeographic information, when combined with information furnished by the scant fossil record, can at best lead to descriptions of broad patterns of distribution and zoogeographic regions and to hypotheses about the essentially long-term processes responsible for them (e.g., Darlington 1957). Such theories, though occasionally suggestive for specific groups, fail to explain the existing taxonomic distributions and the underlying colonization mechanisms for most islands. They neglect the short-term, even daily events that largely determine the parameters of colonization on many islands. Such events become decisively more important than evolution as distance of island from source area decreases. In particular, the classical zoogeographic methods do not provide a test for the existence of an equilibrium number of species or for the accuracy of equation (1).

The literature on biotic dispersal, both anecdotal and systematic, provides information on the relative importance of active and passive transport and a wealth of data on the specific agents of passive transport (e.g., Wolfenbarger 1946). Certain cases of overseas dispersal have even been traced to specific meteorological events (French 1964). For no island, however, is the time course of colonization by even a large fraction of the inhabitants known. The large number of records of long distance dispersal implies that immigration rates to islands are probably high, especially for organisms capable of passive transport by wind. But the shape and determinants of the immigration curve cannot be deduced. At best a lower limit might be given.

In the recent studies of Surtsey, a new volcanic island near Iceland, there has been a deliberate attempt to document the colonization process from

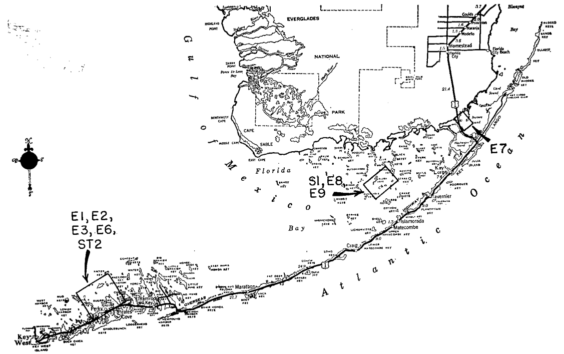

FIG. 1. The southern tip of Florida and the Florida Keys. The rectangles enclose the experimental areas shown in detail in Figures 3–5.

thropods of the Florida Keys with the assistance of Robert Silberglied. This collection enabled us to identify the arthropods on the experimental islands, and it provided a measure of the size and composition of the species pool of the presumed source area, the entire Florida Keys.

Animal diversity on the small mangrove islands proved to be adequate for statistical purposes. About 75 insect species (of an estimated 500 that inhabit mangrove swamps and an estimated total of 4,000 that inhabit all the Keys) commonly live on these small islands. There are also 15 species of spiders (of a total Keys complement of perhaps 125 species) and a few scorpions, pseudoscorpions, centipedes, millipedes, and arboreal isopods. At any given moment 20–40 species of insects and 2–10 species of spiders exist on each of the islands.

Many birds visit the islands either to roost or to forage, but very few nest there. The only birds that bred on our islands during the course of the experiment (1966–68) were one or two pairs each of the Green Heron, White-crowned Pigeon, and Gray Kingbird. Snakes (mostly water snakes of the genus *Natrix*) occasionally swim to small mangrove islands, and raccoons visit islands located on shallow mud banks. These vertebrates were not included in the censuses.

On the basis of their distance and direction from the nearest source area, their size, and their accessibility, the islands listed in Table 1 were chosen for defaunation. Two islands (E6 and E10), one each in the vicinity of the two groups of experimental islands, were selected to serve as control islands; and they were censused at the same time as the experimental islands. In order to ascertain whether any long-range change had occurred in the general fauna of small mangrove islands in Florida Bay during the course of the

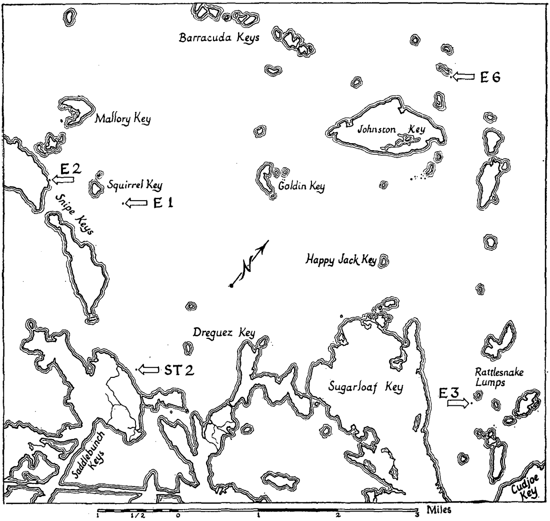

FIG. 3. Map showing the location of the experimental islands of series 1.

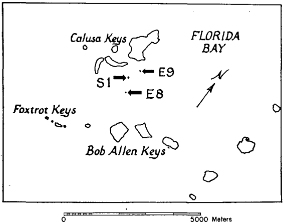

FIG. 4. Map showing the location of the experimental islands of series 2.

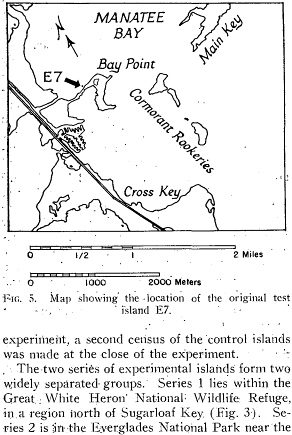

FIG. 5. Map showing the location of the original test island E7.

experiment, a second census of the control islands was made at the close of the experiment.

The two series of experimental islands form two widely separated groups. Series 1 lies within the Great White Heron National Wildlife Refuge, in a region north of Sugarloaf Key (Fig. 3). Series 2 is in the Everglades National Park near the Calusa Keys north of Islamorada (Fig. 4). E7, which was chosen primarily to test a method of defaunation, is located in Barnes Sound south of the Glades Canal (Fig. 5).

The islands were also selected to show as much variation as possible in the degree of isolation from the immigrant sources. The coefficient of correlation for island series 1 between "distance from nearest source" and "number of arthropod species" is —0.83, indicating the operation in the original faunas of the distance effect as defined by MacArthur and Wilson (1967). Qualitative differences in faunas of increasingly distant islands were even more striking than quantitative ones. For many groups—especially ants and spiders—the distance effect is so regular that one can guess not only the species number but also the approximate species composition. For example, centipedes and pseudoscorpions were found almost exclusively on islands of less than 200 m distance from the nearest large island.

Islands of this minute size can be remarkably long lived. All *Rhizophora mangle* trees, and particularly those on low, small islands, have numerous aerial roots: both brace roots growing out from the main stem and prop roots growing down from branches. The latter can emerge from as high as 4 m above the water (LaRue and Muzik 1954) and in time can become as thick as the main stem. *Rhizophora* trees reproduce viviparously, their seeds growing on the tree until they become large, long, pointed seedlings. When they drop, frequently from the upper canopy, some evidently plant themselves where they fall (Davis 1940). Mangrove swamps are often quite thick, and on small islands there may be several trees. Stems, thickened prop roots, and brace roots in-

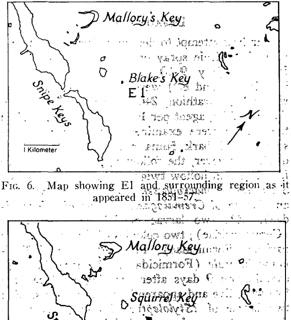

FIG. 6. Map showing E1 and surrounding region as it appeared in 1851–57.

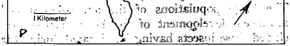

FIG. 7. The same region shown in Figure 6 as it appeared in 1964.

termingle and reproduce themselves so that it is impossible to distinguish how many trees are present, which are which, which is the initial one (even if it is still present), and which are the main stems.

Maps of the Florida Keys, especially of the Sugarloaf Key-Key West area, have been remarkably detailed and accurate with respect to small mangrove islands for at least a century. These tell us that E7 and all the islands in series 1 have existed at least 25 years. The other experimental islands were not mapped in sufficient detail to determine longevity. The size and shape of individual islands may change, even drastically, but in general the islands survive the climatic catastrophes to which they are repeatedly subjected. For example, Figure 6 shows E1 (Blake's Key) and surrounding areas as it appeared in 1851–57, while Figure 7 shows the same island region on the Coast and Geodetic Survey map of 1964. It therefore seems reasonable to assume that the faunas found initially on the experimental islands were the product of many years' colonization. Our experiments have subsequently shown that the minimum ages of the islands greatly exceed the time required to reach species equilibrium from a start of zero species (Simberloff and Wilson 1969).

DEFAUNATION

Our first attempt to defaunate islands made use of an insecticide spray of short-lived residual effect. On July 9–10, 1966, two experimental islands (E1 and E2) were sprayed until dripping with 60 g parathion, 240 g diazinon and 180 g Pylac sticking agent per 100 l fresh water. When the islands were examined 1 day later, all the surface and bark fauna and most borers were dead. However, the following live animals were found in thin hollow twigs. E1: one adult wasp, *Scleroderma macrogaster* (Bethylidae); workers and larvae of *Crematogaster ashmeadi* (Formicidae). E2: two larvae of ?*Styloleptus biustus* (Cerambycidae); two colonies of *Paracryptocerus varians* (Formicidae); and one colony of *Tapinoma littorale* (Formicidae). A more thorough examination 9 days after spraying produced the following live and apparently healthy insects. E1: two larvae of ?*Styloleptus biustus* (Cerambycidae). E2: one larvae of ?*Styloleptus biustus* (Cerambycidae); one lepidopteran larva; and two colonies of *Xenomyrmex floridanus* (Formicidae). The large populations of the ant colonies and advanced development of the beetle larvae precluded these insects having immigrated during the 9 days following spraying.

The results on E1 and E2 showed that a spray cannot be expected to penetrate all the hollow twigs of a *Rhizophora* island. Some twig dwellers will probably survive, particularly if they inhabit narrow twigs (*Tapinoma* and *Xenomyrmex*) or else pack their tunnels tightly with powdery excreta (*Styloleptus*). Had we attempted to kill these survivors by using a spray with a long-lived or more powerful residue, we would have postponed the beginning of the colonization curve, since immigrants may be killed by the residue. Because we had to be certain that all colonists, or at least all but those belonging to a small number of known taxa, would be destroyed immediately, we abandoned the spray technique.

We turned next to the more difficult alternative technique of fumigation. The method has the obvious advantages that the residual effect of a gas is negligible, and even the inhabitants of hollow twigs are contacted. This is the standard method used by professional exterminators on termites and other wood-boring insect pests.

The fumigation of living plants is a relatively uncharted area. The biochemical effects of fumigants on plants are poorly known, damage usually being described in terms of the physical appearance of the plant shortly after fumigation (Page and Lubatti 1963). To our knowledge, the only prior fumigation of red mangrove trees was by B. P. Stewart (pers. comm.), who used methyl bromide on small plants. With 32 kg/1000 m^3 for 2 hr at 32°C and 40 kg/1000 m^3 for 2 hr at 27°C he found that all insects apparently were killed, although some did not die until 48 hr after fumigation. Mortality of cockroach eggs was unrecorded in Stewart's study. Damage to the plant was limited primarily to young leaves and twigs, a result that is in accord with the general finding of Page and Lubatti (1963) that the growing stages of both plants and insects are the most susceptible to fumigation.

In our preliminary trials we were limited by the fact that fumigants highly soluble in water, such as hydrogen cyanide, could not be used. These substances would be expected either to leave the fumigation tent through the water or to concentrate to an unknown extent in the water under the island. Either effect would greatly complicate the maintenance and measurement of gas concentration. Consequently, the following four relatively insoluble fumigants were tried: Pestmaster Soil Fumigant-1 (methyl bromide 98% wt, chloropicrin 2% wt); Acritet 34-66 (acrylonitrile 34% vol, carbon tetrachloride 66% vol); Dow Ethylene Oxide (ethylene oxide 100%); and Vikane (sulfuryl fluoride 95% wt, inert ingredients 5% wt). Field tests were performed on small *Rhizophora* trees in Matheson

Hammock Park, Coral Gables, by National Exterminators of Miami, Florida, under the direction of Steve Tendrich in consultation with the authors. Additional tests on the mortality of mangrove colonists were performed at National Exterminators' laboratory in Miami.

With the temperature outside the fumigation tent remaining at 24°–29°C, we determined which duration-concentration intensities caused no more than bearable damage to the tree yet were lethal to all the mangrove arthropods. Acritet, Vikane, and ethylene oxide caused extensive, apparently irreversible damage to red mangrove and were rejected. However, methyl bromide at 22 kg/1000 m^3 for 2 hr caused browning of only about 10% of the leaves 1 week after treatment, with no visible later effects. This duration and concentration killed all the mangrove inhabitants (including such resistant forms as roach eggs and lepidopteran pupae) with one possible exception. When data from all tests at this duration-concentration are lumped together, only 95% of cerambycids and 80% of weevils were dead when dug out of their burrows 1–10 days after fumigation. The remainder all died within 2 days of removal. It is tempting to ascribe the death of these few larvae to a delayed effect of the fumigant. However, a control experiment consisting of the removal of five unfumigated cerambycid larvae (*Styloleptus biustus*) from their respective burrows caused death within 5 days without any additional treatment. Monro and Delisle (1943) report that many insects are active soon after exposure to methyl bromide but succumb in time (some lepidopterous larvae surviving for 2 months), and that this delayed effect is especially common in fumigations at the low concentrations used in our own field tests. This peculiarity is confirmed by Chisholm (1952) for Japanese beetle larvae and other insects. Of at least equal importance, the results from our experimental islands (Simberloff and Wilson 1969) strongly suggest that the cerambycids were eliminated by the fumigation treatment. We therefore conclude that even the deep-boring beetle larvae were very probably killed by the treatment.

The overt physical damage to the trees consisted of a browning of leaves and shoots and occasional heavy oozing of sap. At 61 kg/1000 m^3 the leaf browning was manifest upon tent removal, but at 35 kg/1000 m^3 and less there was little or no immediate browning. The effect became evident at about 24 hr and worsened in terms of fraction of leaves browned through 72 hr, by which time up to 90% of the leaves were brown and after which no further browning occurred. Browning did not occur randomly throughout the canopy. Instead, whole sections of the tree became completely brown while others remained almost unscathed. The upper canopy was always more severely browned, but there seemed to be no other consistent damage pattern.

Abscission of the dead leaves began within a week and, often aided by wind, was usually complete within 8 weeks. At this time damaged trees looked superficially dead except for remaining green sections. Closer examination showed that the damaged trees could be conveniently divided into three classes, as follows:

For those trees where browning of leaves and shoots appeared complete by 72 hr the damage was irreversible. Within a few months bark began to peel and twigs with green wood could not be found. A year later there was no evidence of life. Island E8 is in this class. In the second category, which includes only E7, a large majority of the leaves and shoots were browned and died, while a small section remained green. In the third category, the trees were less severely damaged (60% or fewer browned leaves). Green sections remained unchanged, while leaf abscission in most of the damaged sections was accompanied by the sprouting of new shoots and leaves from almost all branches. Within 2 months the trees appeared normal except for occasional leafless patches in the extreme upper canopy. Island E1, which 2 days after fumigation appeared to have about 50% brown leaves, recovered after 1 month to the extent that it did not appear to have incurred more damage than similar trees do during heavy storms, and 2 months after defaunation seemed quite normal except for a small bare patch in the upper canopy. At no time did its bark crack or peel.

In most damaged trees of the first two classes—where either the whole tree or all but a small section was killed—there was copious oozing of sap for up to a week after fumigation. Such oozing was never observed in untreated trees, nor in those fumigated trees which showed good leaf replacement.

The action of methyl bromide on living plants has been studied rather extensively by several authors. Mainwaring (1961) examined the physiological responses of several plants to methyl bromide, and his numerous observations imply that its major effect is auxin inhibition. The damage we observed seemed too drastic and certainly too immediate to be attributed solely to auxin inhibition, although the presence of such a biochemical action cannot be ruled out.

Whatever the effect of methyl bromide on *Rhizophora mangle*, it apparently had the expected Q_{10} of 2–3. Our initial tests in Matheson Hammock were conducted on small plants well shaded

TABLE 3. Extent of damage to foliage and subsequent recovery on experimental islands

Island	Fumigation date	Time	Extent of damage (burnt leaves)	Damage location	Recovery of foliage
E1	3/13/67	day	50%	general	complete in 2 months, except for extreme upper canopy
E2	3/7/67	night	10%	upper canopy	complete in 2 months
E3	3/17/67	night	5%	upper canopy	complete in 2 months
E7	10/10/66	day	85%	all except one section	none
E8	4/17/67	night	100%	complete	none
E9	4/7/67	night	20%	upper canopy and one other section	little in upper canopy complete elsewhere in 2 months
ST2	4/20/67	night	5%	scattered	complete in 2 months

with mudscrews or stakes, depending on the substrate. Using a block and tackle, one man on the tower and one on the island lifted the rolled tent until it formed a triangle over the island. The tent was then carefully unrolled down the guide wires until the island was covered (Fig. 9). It was impossible to unfurl the tent from the tower in winds greater than 8 knots. Sandbags and stakes were used to keep the tent edges submerged.

Equipment used in the tower method was identical to that described already for the scaffolding method, and was similarly situated. The procedure was identical except that gas was administered from 0.5-kg cans and concentration and duration were increased to 28–33 kg/1000 m^3 for 2.5 hours on all islands but E1. After fumigation the methyl bromide was released through tent seams as with scaffolding, but in the tower system tent removal was more difficult. At low wind speeds the tent could be laboriously refurled and gradually lowered to the boat. We fortuitously discovered that high winds, instead of causing extensive damage as we expected, could actually aid tent removal. The windward side of the tent was lifted by poles to about 3 m above water, whereupon sufficient wind entered the tent to lift it up over the tree and to drop it, partly extended, into the water on the leeward side of the island.

E1 was fumigated in the daytime. For all remaining islands the tent was unrolled no earlier than 60 min before sundown, the fumigation was conducted between 8:00 and 12:00 pm, the gas was removed by 1:00 am, and the tent was either off the island or refurled within 90 min of dawn. Effects on the mangrove trees of the fumigated islands are noted in Table 3.

All islands were examined immediately after tent removal. No living animals at all were found on E1, E2, E8, and E9. A single live curculionid larva was found on E3. On ST2, 1 living and at least 100 dead polyxenid millipedes (*Lophoproctinus ?bartschi*) were found. Although we have no further direct evidence and know of no work on methyl bromide fumigation of millipedes, we suspect that all millipedes not destroyed immediately were killed by the delayed effect of methyl bromide discussed earlier.

In sum, we feel that this fumigation technique killed all mangrove arthropods with the single remotely possible exception of deep-boring beetle larvae.

MONITORING TECHNIQUE

Precautions were taken at all monitorings[2] to prevent contamination of the experimental islands. Boats were never brought in contact with the islands and only seldom tied to them; usually they were anchored at least 12 m away. Before wading to an island, experimenters examined clothing, equipment, and persons for animals, which were destroyed. To lessen the chance of phoresy, investigators simply immersed themselves briefly or sprayed themselves with "Off" insect repellent. All equipment used on the island was sprayed weekly with a short-lived insecticide.

The absence of supratidal land, except around E9, greatly simplifies the environment of the experimental islands. The arboreal substrate may be arbitrarily divided into hollow twigs, living branches and twigs, dead bark and tree holes, leaves and flowers, green shoots, and fruits. Because of the extremely small size of the experimental islands it was possible to study most of these microhabitats all but exhaustively for the pre-defaunation censuses. A typical example is the survey of E3, where we broke and examined 3,500 of an estimated 5,000 small hollow twigs, collected

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[2] The term "monitoring" is used to designate one or more of the censuses of species, conducted for a period of 17–20 hr during the course of the experiment. In the present series of articles, monitoring, census, and censusing are used interchangeably to refer to the listing of species.

90% of the fruits, examined virtually all of the leaves, and looked under at least 80% of the pieces of dead bark. *Rhizophora* has numerous limbs and our islands were relatively low, so that we were able, by climbing carefully, to examine the canopy right to the top.

The fumigation procedure itself gave added evidence of the completeness of our original surveys. The fumigant included 2% chloropicrin, which drives out even deep-boring and hollow-twig-dwelling arthropods (cf. Lauck 1965). The animals either fell into the water or remained hanging from branches by spines or silk, tenuously and conspicuously. Those which fell generally remained afloat and, when a tent seam was opened after fumigation, flowed out in masses where they were collected on a screen.

The chloropicrin technique was especially effective on E8, E9, and ST2, and the results indicated greater densities of both insects and spiders than we had suspected. Only on E8, however, were animals found that had not been noted in the original surveys. These consisted of four beetles:

Staphylinidae: gen. sp.
Carabidae: *Bembidion* sp. nr. *contractum*
Carabidae: *Tachys occulator*
Oedemeridae: *Oxacis* sp.

Of these the first three were apparently living in a patch of temporarily supratidal mud, which was submerged again 2 weeks later during a strong wind. The *Oxacis* were encountered only on the fumigation tent, and even their status as "transients" is doubtful.

Defaunated islands were censused for approximately 2 days every 18 days. At each census period approximately 10% of all hollow twigs were broken, and with this treatment the number of hollow twigs seemed to remain constant throughout the experiment. Only when gentle lifting failed to allow vision was dead bark removed, and then only a part was peeled off. Small amounts of carbon tetrachloride and ammonia, and tapping with a steel probe were used to drive animals out from underneath bark and inside hollow twigs without damage to tree or colonist. Although the pre-defaunation searching methods had been drastic, care was taken following defaunation to prevent the censusing from being destructive and from altering the proportions of the respective microhabitats on an island.

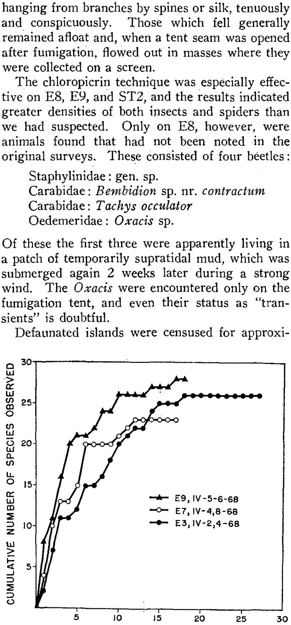

FIG. 10. Cumulative species counts during individual censuses on three of the experimental islands.

Most colonists could be identified in the field because of the small subset of the Keys fauna which invades small mangrove islands and the completeness of our reference collection. Those that could not be recognized with certainty were treated in one of two ways. If the animal in question was obviously part of a sizable population, as with many psocopterans and thrips, a small collection was made that did not exceed 2% of the estimated minimum size of the population. When an unknown arthropod was not part of a large population, we photographed it.

It was quickly discovered that the rate of discovery of new species during each censusing period, although at first very high, declined approximately linearly to near 0 at about 14 man-hours of searching. A very few species are expected to appear from immigration within the monitoring period. Figure 10 depicts the cumulative number of species observed vs. time for three representative monitorings. Different sizes of islands, weather conditions, and especially varying population sizes caused minor differences in the curves from island to island and from time to time; but despite great changes in the numbers of species through the course of the experiment, the curves remained remarkably similar in shape. The censusing period was therefore chosen to last between 17 and 20 man-hours.

Because of the simplicity and very small size of the experimental islands, and because several nocturnal censuses located no new species, we felt that all colonists having crepuscular or nocturnal activity were being recorded during the diurnal monitoring. The anyphaenid spider *Aysha* sp. and ant *Paracryptocerus varians* are both strictly nocturnal, yet both were recorded during the day in their retreats. Similarly the crepuscular braconid wasp *Macrocentrus* sp. and largely nocturnal ants *Camponotus floridanus* and *Tapinoma littorale* were repeatedly observed.

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